The Philippine slime molds after Dogma's 1975 list – How far have we been?

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Abstract

One of the pioneering taxonomic works about the Philippine slime molds (that includes the myxomycetes and dictyostelids) were the annotated check list reported by Dogma in 1975 published in the Kalikasan - Philippine Journal of Biology. This report meaningfully contributed to the succeeding studies conducted with the Philippine slime molds after almost four decades of stagnancy. Hence, this review paper tackles how the studies regarding the Philippine slime molds progressed since Dogma's 1975 annotation, particularly in further understanding the ecology and systematics of these fungus-like protist. At present day, the total number of myxomycetes species in the Philippines is 159 while the number of records for dictyostelids is 12.

Keywords: amoebozoa, Asian Palaeotropic, myxomycetes, species list, tropics

Introduction

In nature, microorganisms are often feed upon by another microorganism. As such, one of the known terrestrial microbial predators are the slime molds. For this review, we will cover the two groups of slime molds – the plasmodial slime molds and the cellular slime molds. Both exhibited an almost similar feeding life cycle yet they have intricate life cycles and morphologies that fascinate many non-experts and fungal enthusiasts around the world.

Myxomycetes are representatives of the plasmodial slime molds. They are an enigmatic group of fungus-like protists that usually begins with the dispersal of millions of spores from a single fruiting body in the environment. After germination of spores, amoeba will then appear. If these amoebas landed in a terrestrial environment, they apparently become either as swarm cells or myxamoebas. The myxamoeba is adept at experiencing multiple cell divisions through mitosis while the swarm cells do not undergo such cell division (Everhart & Keller, 2008;

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Date Submitted: 01 July 2019 Date Accepted: 18 February 2020 or the swarm cells turns to its resting stage called the microcyst. Sexual reproduction of myxomycetes then begins when two compatible mating haploid cells fuse and form a diploid zygote (see review by Clark & Haskins 2013). The formed zygote will then undergo a period of development that leads to the formation of a multinucleated network of giant cell mass capable of cytoplasmic streaming called the plasmodia (Everhart & Keller, 2008; Clark & Haskins, 2016). This assimilative, multinucleated, giant cell mass is characterized to be the animallike feature in its whole life cycle. This is attributed to the plasmodium's ability to move via cytoplasmic streaming across different substrata so that it can prey on microorganisms (Gray & Alexopoulos, 1968; Dagamac & dela Cruz, 2015). This predatory nature of the plasmodium maintains the balance of soil microbiota in the soil ecosystems (Feest & Madelin, 1985). Likewise the uninucleated cells of myxomycetes, plasmodia embody the capability to form a dormant stage under harsh, stressful and unfavorable condition, called the sclerotia (Martin & Alexopoulos, 1969). However, plasmodia can also decide not to go dormant but rather shift into a more stable reproductive strategy by transforming into a fungus-like fructification that would again develop the haploid spores through a reductive division called meiosis. The fruiting bodies are what make the

myxomycetes appear to be like fungi, besides being found on

Stephenson & Stempen, 1994). Once conditions become unfavourable, i.e., lack of food, overcrowding, accumulation of

toxic metabolic by products, drought or drier conditions, and/or

wide temperature fluctuations, either the amoeboflagellated cells

similar habitats where fungi are usually thriving (Everhart & Keller, 2008; Dagamac et al., 2015a). Myxomycetes also follow its dispersal ecology (Schnittler et al. 2017a). Fruiting bodies may vary in forms which can either be a sessile or stalked sporangium that has definite size, shape, or color (Stephenson & Stempen, 1994). These morphological characters are commonly used as diagnostics to determine a particular species of myxomycetes. Moreover, in spite of having distinct morphological features, comprehensive microscopic examinations should also be done in order to examine other micro-morphological structures like the spores and capillitium.

Dictyostelids, as the most diverse representatives of cellular slime molds, are abundant in the humus layer of forest soils that are rich in bacteria on which they feed (Cavender & Raper, 1965a; Cavender & Raper 1965b). Their presence in soil limits the growth of bacterial population and thus, makes dictyostelids an important biological vector that maintains the balance of microbial activities in the soil environment. Just like myxomycetes, the life cycle of dictyostelids is complex and involves both unicellular and aggregated multicellular stages. It includes three important components: (i) a vegetative feeding phase, (ii) a starvation phase, and (iii) the fruiting development phase. As described by Romeralo et al. (2012), the vegetative feeding phase involves a unicellular, uninucleated amoeba with bulbous pseudopodia that divides by mitosis. The individual cell feeds on bacteria, often attracted to the chemical signals released by the bacteria. During a starvation phase due to lack of food, individual amoeba encysts itself, forming a microcyst. Interestingly, dictyostelids can also enter the sexual cycle, and by sexual fusion form a recombinant amoeba which attracts haploid amoebae. These haploids are cannibalized by the zygote, which after this, transforms into a macrocyst. In the event of bounty, the macrocyst release recombinant amoeba. The last phase begins with the aggregation of individual amoeba forming a "slug"-like pseudoplasmodum that moves in unison and acts just like a social organism. The aggregation then leads to the development of multicellular fruiting body and formation of spores. Just like the plasmodial slime molds, these spores can remain viable for an extended period of time, and when conditions again become appropriate, amoebae emerge from

For the Philippines, one of the earliest reports about slime molds was written by Dr. Irineo J. Dogma Jr. in the late 70s. This early taxonomic works serve as one of the baseline information of current diversity studies carried out for the country during the last decade. Hence, this review tackles the advances in taxonomic work about the Philippine slime molds.

Updating Dogma's Report

The publication of Dogma (1975) enumerated 46 myxomycetes species coming from 20 genera. On that report, the following comments were highlighted: (1) the criticism to Uyenco's (1973) claim that there was no previous report of myxomycetes for the Philippines, (2) the monograph of Martin & Alexopolous entitled The Myxomycetes already credited 22 species in the country, and (3) the plan of Don Reynolds to create a comprehensive list of myxomycetes collected all over the Philippines. For the latter, it took quite several years for it to be accomplished, as it took another 6 years for Don Reynolds to report the 107 myxomycetes for the Philippines (Reynolds, 1981). After 35 years, a new, annotated list of myxomycetes species for the country was published by Dagamac & dela Cruz (2015). From that report, several remarks about Reynold's (1981) comprehensive list were made: (1) an unidentified species of Didymium that closely look like D. squamulosum was included, and (2) Stemonitis nigrescens and S. smithii were considered as synonyms of S. axifera and S. fusca, respectively. These corrections from the updated check lists of Dagamac & dela Cruz (2015) were incorporated updating at that time a total of 150 myxomycete species for the Philippines.

This number came from several publications produced from 2009 - 2015 by the UST-RCNAS Fungal Biodiversity, Ecogenomics and Systematics (FBeS) group (https:// ustfungalbiodiversitylab.wordpress.com/). Most of the research group's taxonomic surveys were carried out in several forested provincial areas and islands of the country (Fig.1) like Pangasinan (Kuhn et al., 2013a; Kuhn et al., 2013b, Rea-Maminta et al., 2015), Lubang Islands, Occidental Mindoro (Macabago et al., 2012), Polilio Islands, Quezon (Viray et al., 2014), Puerto Galera, Oriental Mindoro (Dagamac et al., 2015b), Bataan, Cavite and Subic (dela Cruz et al., 2010; dela Cruz et al., 2014). A new species, Craterium retisporum G. Moreno, D.W. Mitch. & S.L. Stephenson was described from specimens collected in Anda Island (Moreno et al., 2009). Moreover, that report also included 8 new records from Bicol Peninsula (Dagamac et al., 2017a) that was initially only available as online reprint version in 2015 since it was part of the special volume issue about myxomycetes of the journal Nova Hedwigia in 2017. Besides the species listings, the FBeS group carried out extensive ecological surveys on unexplored protected montane forest of the country (Fig. 2), i.e., in Mt. Arayat National Park, Pampanga (Dagamac et al., 2011; Dagamac et al., 2012; Dagamac et al., 2014), Mt. Makulot, Batangas (Cheng et al., 2013), and Mt. Kanlaon, Negros Island (Alfaro et al., 2015). Moreover, surveys in various natural ecoparks and national parks (Fig. 2), i.e., La Mesa ecopark in

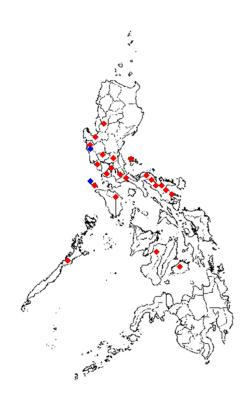


Figure 1. Map of the Philippines showing the areas were myxomycetes (red diamond) and dictyostelids (blue diamond) were surveyed based on publications from 2009 - 2019.

Quezon City (Macabago et al., 2010), Atimonan trail of Quezon National Park in Quezon (Dagamac et al., 2015a), Hundred Islands National Park in Pangasinan (dela Cruz et al., 2011), Mt. Palay-Palay National Park in Cavite (Corpuz et al.,2012), Biak na Bato National Park in Bulacan (Atayde et al., 2012) were carried out. After the report of Dagamac & dela Cruz (2015) from Reynold's report, a number of papers regarding Philippine myxomycetes were published in which other habitat types such as grasslands (Carascal et al., 2017) and coastal forests (Macabago et al., 2016). As previously mentioned, a special issue about myxomycetes was published by the international journal Nova Hedwigia in 2017. Together with the paper from Bicol Peninsula, two additional papers from this journal reported rapid diversity assessments conducted in the Philippines. The first one is the first report of myxomycete survey in the karst forests of Puerto Princesa Subterranean River National Park, Palawan, Philippines (Pecundo et al., 2017) and the second one is the report about the possible role of natural disturbances in transformation of vegetation in Bohol, Philippines (Macabago et al., 2017). The latter paper reported an additional eight new records namely Comatricha elegans (Racib.), G.Lister, Comatricha laxa Rostaf., Didymium bahiense Gottsb., Physarina echinospora, K.S.Thind &

Manocha, Physarum bitectum G.Lister, Physarum sulphureum Alb. & Schwein., Physarum serpula Morgan, and Physarum straminipes Lister. A recent publication about forest patches in the municipalities of Calauan and Los Baños, Laguna by Bernardo et al. (2018) added a new record of the rare species Cribraria lepida Meylan as new for the country. Hence, currently for this review from the 46 taxa initially reported by Dogma in 1975 and the recent annotated list of 150 taxa by Dagamac and dela Cruz (2015), the Philippines now have a total of 159 myxomycetes species, collected in considerable number of terrestrial habitats (Fig.2). This number is relatively more than those reported in other ASEAN countries like Brunei (26 taxa, Ing & Spooner, 1998), Cambodia (30 taxa, Ko Ko et al., 2015), Indonesia (119 taxa, Rosing et al., 2011), Laos (44 taxa, Ko Ko et al., 2013), Malaysia (82 taxa, Rosing et al., 2011), Myanmar (67 taxa, Ko Ko et al., 2013), Singapore (92 taxa, Rosing et al., 2011), Thailand (145 taxa, Dagamac et al. 2017b) and Vietnam (131 taxa, Redeña-Santos et al., 2018). And just recently, a webpage on Philippine myxomycetes was created (https://philmyxos.wordpress.com/).

The report of Dogma in 1975 about the status of dictyostelids in the Philippines was an addition of a new record for the country. On that report, he stressed his successful isolation of the species Dictyostelium rosarium from Los Baños, Laguna. Before this, Dogma & Blancaver (1965) initially reported D. discoideum, D. mucoroides, Polysphondylium pallidum (currently known as Heterostelium pallidum (Olive) S. Baldauf, S. Sheikh & Thulin), and Polysphondylium violaceum as the first dictyostelid isolates for the Philippines. Five more species were reported for the country by Cavender (1976) who worked at Corregidor Island and Ipo Dam in Luzon and from Lambuan in Panay Island, the Visayas: Acytostelium subglobosum, Dictyostelium lacteum var. papilloideum (currently known as Tieghemostelium lacteum (Tiegh.) S. Baldauf, S. Sheikh & Thulin), Dictyostelium mucoroides var. stoloniferum (Dictyostelium mucoroides Bref.), Dictyostelium polycephalum (Coremiostelium polycephalum (Raper) S. Baldauf, S. Sheik, Thulin & Spiegel), Dictyostelium purpureum, and one unidentified species of Dictyostelium sp., Thus, there are 10 identified taxa of dictyostelids known for the Philippines after 1976. For over 30 years, no studies regarding Philippine dictyostelids followed until Yulo and dela Cruz (2011) studied the cellular slime molds of Lubang Island, Occidental Mindoro and identified seven species, two of which, Dictyostelium aureostipes (Cavenderia aureostipes (Cavander) S. Baldauf, S. Sheikh & Thulin), and D. laterosorum (Polysphondylium laterosorum (Cavender) S. Baldauf, S. Sheikh & Thulin), were reported for the first time in the country, bringing the total number of dictyostelids identified in the Philippines to 12. The

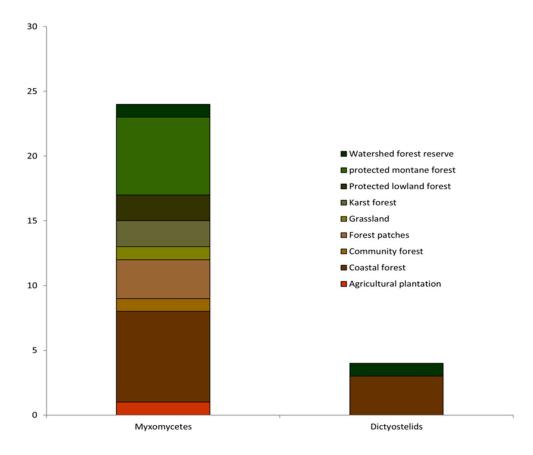


Figure 2. A stacked graph showing the major terrestrial habitat types that was investigated for myxomycetes and dictysotelids based on the number of publication (y axis) accounted from 2009 - 2019.

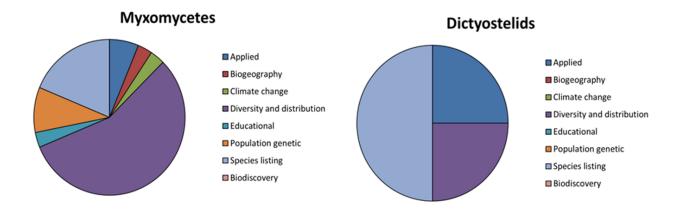


Figure 3. Distribution of scientific themes used in the study of Philippine slime molds

number of species is relatively comparable, albeit still very low, to other ASEAN countries. Thailand, for example, reported 17 species from studies carried out in Chiang Mai, Nakhon Si Thammarat and Songkhla provinces (Cavender 1976, Seephueak & Petcharat 2014). Vadell et al. (2018) has recently described five new species from soil samples collected in four localities in Northern Thailand.

New approaches in studying Phillipine slime molds

From the annotations on the several myxomycete collections in the country that Dogma (1975) and Reynolds (1981) conducted, the scope of new techniques and habitats to study plasmodial slime molds in the Philippines is now immensely growing. Most of the recent publications showed that majority of the taxonomic approach used for myxomycetes is still based on morphology with a slow increase to conduct modern molecular techniques. Nonetheless, besides doing pure descriptive studies about the Philippine myxomycetes, a number of other scientific themes have been conducted for myxomycetes (Fig. 3). Efforts to disentangle the ecological role and biogeographic distribution of myxomycetes not just at a regional scale (Almadrones-Reyes et al., 2019), but also at a wider global perspective (Schnittler et al. 2017a) are indeed a budding feat. During the last years, many unexplored microhabitats were investigated for myxomycetes. The study of Dagamac et al. (2010) on the barks of Samanea saman yielded 5 new records of corticolous myxomycetes. Similar with other substrates that were reported in other tropical countries, i.e. lianas (Wrigley de Basanta et al., 2008), agricultural leaf litters (Redeña-Santos et al., 2017), Philippine myxomycetes were also reported in indigenous plant substrates like grasses (Cogon, Carascal et al., 2017) or dead inflorescence (Pecundo et al., 2017). With many more possible plant communities that can be suitable microhabitats for myxomycetes in the tropics, an opportunity to possibly understand substrate specificity (Redeña -Santos et al., 2017) and realized niches (Almadrones-Reyes et al., 2018) of some tropical myxomycetes are new avenues for research in the Philippines.

Moreover, the global distribution patterns of myxomycets are still a debatable field. Recently, data coming from the collective myxomycete surveys conducted in Southern Philippines contributed significantly in understanding *moderate* endemicity concept among tropical myxomycetes (Dagamac et al., 2017b). Hence, the application of modern models for community ecology (Bernardo et al., 2018; Macabago et al., 2017) and powerful statistical tools (Redeña-Santos et al., 2018; Novozhilov et al., 2018) may aid in revolutionizing many ecological studies to unexplored areas in the Philippines.

Ecological concepts like island biogeography, temporal and spatial variation, and dispersal ecology are some exciting topics to dwell on for the future. Nonetheless, myxomycete studies are now investigated with some state of the art techniques that include DNA barcoding (Dagamac et al., 2017c; Schnittler et al., 2017b; Shchepin et al. 2017) or next generation sequencing (Shchepin et al., 2019). In fact, in the recent publication of Dagamac et al. (2017d), high molecular diversity was seen in *Hemitrichia serpula* populations coming from Southeast Asian collections including the Philippines. If this is the case, gene flow among countries that are separated by geographical barriers are interesting question to answer for Philippine myxomycetes.

A new trend nowadays for conservation biology and environmental sciences is the possible effects of climate change to many biological species. As a major component of soil biota (Stephenson et al., 2011), understanding the range dynamics of myxomycetes in nature should also be given concern by applying GIS-based niche modelling (Stephenson et al.2019; Rojas et al., 2015). In fact, the recent publication of Almadrones -Reyes & Dagamac (2018) about the habitat suitability modelling of a cosmopolitan myxoymcetes in the Philippines, Diderma hemisphaericum, points the possible expansion of the species. Using the current occurrence records for the country, it seems that many areas that are facing the threat of deforestation, urbanization and land-use change in the Philippines e.g., Cebu, Sarangani, National Capital Region can extremely disturb the species distribution of myxomycetes. Nevertheless, applying this new approach of species distribution modelling to myxomycetes can suggest not only which areas should be prioritized in future myxomycetes surveys, i.e. Mindanao area and many islands of Visayas, but also, which habitats are in need of immediate conservation strategies. Furthermore, practical applications of Philippine myxomycetes with regards to the potential for bioremediation (Rea-Maminta et al., 2015) and enzyme production (Macabago et al., 2014) have been successfully reported, and thus, should also be considered for any future studies.

However, very little progress has been done with the dictyostelids in the Philippines which most taxonomic approach is still purely morphological. In addition to the species listing carried out in Lubang Island, Occidental Mindoro by Yulo & dela Cruz (2011) and in Subic Bay Forest Reserve, Zambales by dela Cruz et al. (2011), there was also an attempt to look at the diversity and distribution of dictyostelids (Yulo & dela Cruz, 2012a). An effort to study the bacterial and yeast feeding preferences of cellular slime molds was also conducted by Yulo and dela Cruz (2012b). But there is so much work needed in our studies of Philippine dictyostelids. With a recent discovery of five new species of dictyostelids in Thailand (Vadell et al.,

2018), it is also not surprising that new taxa of cellular slime molds could be found in the country, a place known for its megadiversity.

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